NOTE ON THE INFLUENCE OF TEMPERATURE UPON THE RATE OF THE HEART-BEAT IN A CRUSTACEAN (CERIODAPHNIA).[1]

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1. Arrhenius has shown[2] that the velocity of a chemical reaction increases very much more rapidly with increasing temperature than any known physical phenomenon. The velocity of a chemical reaction increases about 10 per cent. per degree centigrade rise in temperature while molecular velocity, the electric conductivity of a wire, the elasticity of a solid, the viscosity of a fluid, surface-tension, etc., are much less affected by the same rise of temperature. The viscosity of a fluid, for example, only diminishes about 2 per cent. per degree centigrade rise in temperature. The viscosity of a gas, according to Maxwell's equation for air[3] should increase about 6.7 per cent. per degree centigrade rise in temperature at 15° C.

2. The fact of the extreme variability of chemical reactions with temperature has been applied to ascertain whether given biological phenomena involve chemical reactions or not. Arrhenius[4] and van t'Hoff[5] have shown that the quotient

$$\frac{\text{velocity of reaction at } T_{n+10}}{\text{velocity of reaction at } T_n}$$

is equal to about 2, T_n being the absolute temperature. That is to say, the velocity of a chemical reaction increases about 100 per cent. per ten degrees. Hertwig[6] has found that the rate of development of frog's eggs increases very rapidly with rise of temperature. At Dr. Loeb's suggestion C. D. Snyder[7] investi-

[1] From the Rudolph Spreckels Physiological Laboratory of the University of California.

[2] *Zeitschrift f. Physik-Chemie*, 1899, Bd. 4, s. 226.

[3] "Theory of Heat," 1872, p. 279.

[4] *Loc. cit.*

[5] "Études de dynamique chimique," p. 112, etc.

[6] "Die Zelle und die Gewebe," Bd. II., S. 119.

[7] University of California Publications, Physiology, Vol. 2, p. 125.

gated the influence of temperature upon the rate of the heart-beat and found that the rate of the beat in the heart of the terrapin (*Clemmys marmorata*) is almost exactly doubled by ten degrees rise in temperature between the temperatures 10° C. and 32.5° C. — at lower temperatures the rate is more than doubled by a rise of 10° while at higher temperatures the rate is somewhat less than doubled by the same rise in temperature. Loeb [8] has found that the velocity of artificial maturation in the eggs of Lottia is more than doubled by raising the temperature from 8° C. to 18° C. Other investigations on the influence of temperature upon biological phenomena are being carried out in this laboratory. These observations do not prove that the above-mentioned biological phenomena are entirely chemical in character, but they afford indication that chemical reactions are involved although not to the exclusion of possible concurrent physical changes.

3. It appeared to me of interest, in connection with experiments on the influence of electrolytes on the rate of the heart-beat, of which an account will appear at an early date, to ascertain the influence of temperature upon the rate of the heart-beat in the transparent fresh-water crustacean Ceriodaphnia (?). The organism, after washing in tap-water, was laid in a drop of tap-water in the depression on the glass top of an Englemann gas-chamber, the temperature being regulated by running warm or cold water through the chamber. A thermometer was fitted into the chamber so that the bulb lay directly under the depression in which the organism was placed. A few minutes was always allowed to elapse before the rate of the beat was registered in order to allow the organism to attain the same temperature as the bulb of the thermometer. The beats at room-temperature and at higher temperatures are so rapid that they cannot be counted but have to be recorded by tapping a key which completes a circuit including a signal-magnet, which thus registers a mark upon a revolving drum for every beat, the time being taken with a stop-watch.

4. The following are the experimental results.

[8] University of California Publications, Physiology, Vol. 3, p. 1.

EXPERIMENT 1.

Temperature.	Beats per Second.
24.75°	6.53
20.75°	4.43
15.75°	2.47

EXPERIMENT 2.

Temperature.	Beats per Second
15°	2.53
19°	3.46
23°	4.39
27°	6.11

EXPERIMENT 3.

Temperature.	Beats per Second.
15°	2.63
17°	2.95
19°	3.67
21°	4.87
23°	5.05
25°	6.59
27°	6.10
29°	7.375

$$\frac{\text{Rate at } 25^\circ}{\text{Rate at } 15^\circ} = 2.51; \quad \frac{\text{Rate at } 27^\circ}{\text{Rate at } 17^\circ} = 2.07; \quad \frac{\text{Rate at } 29^\circ}{\text{Rate at } 19_\circ} = 2.01.$$

EXPERIMENT 4.

Temperature.	Beats per Second.
13°	2.22
15°	2.88
17°	3.46
19°	2.95
21°	3.91
23°	5
25°	5.71
27°	6.23
29°	6.15

$$\frac{\text{Rate at } 23^\circ}{\text{Rate at } 13^\circ} = 2.25; \quad \frac{\text{Rate at } 25^\circ}{\text{Rate at } 15^\circ} = 1.98;$$

$$\frac{\text{Rate at } 27^\circ}{\text{Rate at } 17^\circ} = 1.80; \quad \frac{\text{Rate at } 29^\circ}{\text{Rate at } 19^\circ} = 2.08.$$

EXPERIMENT 5.

Temperature.	Beats per Second.	Remarks
11°	2.31	Irregular pauses in diastole accompanied by very slight quick beats.
13°	——	Still irregular.
15°	4.12	Regular.
19°	4.79	"
21°	6.15	"
25°	6.22	"
29°	6.17	"
31°	7.01	Gills stopped.

At 33° the whole animal went into convulsive tremors, and at 35° the heart stopped permanently.

$$\frac{\text{Rate at } 21^\circ}{\text{Rate at } 11^\circ} = 2.66\,; \quad \frac{\text{Rate at } 25^\circ}{\text{Rate at } 15^\circ} = 1.51\,;$$

$$\frac{\text{Rate at } 29^\circ}{\text{Rate at } 19^\circ} = 1.29\,; \quad \frac{\text{Rate at } 31^\circ}{\text{Rate at } 21^\circ} = 1.14.$$

EXPERIMENT 6.

Temperature.	Beats per Second.	Remarks.
11°	2.11	Beat irregular
13°	2.53	" "
15°	2.53	" regular
19°	2.67	" "
21°	4.05	" "
23°	4.80	" "
25°	5.56	" "
29°	6.30	" "
29°	5.33	After a fall and subsequent rise in temperature.

$$\frac{\text{Rate at } 21^\circ}{\text{Rate at } 11^\circ} = 1.92\,; \quad \frac{\text{Rate at } 23^\circ}{\text{Rate at } 13^\circ} = 1.90\,; \quad \frac{\text{Rate at } 25^\circ}{\text{Rate at } 15^\circ} = 2.20\,;$$

$$\frac{\text{Rate at } 29^\circ}{\text{Rate at } 19^\circ} = 2.36\,; \quad \frac{\text{Rate at } 29^\circ}{\text{Rate at } 19^\circ}\text{(second observation)} = 2.00.$$

EXPERIMENT 7.

Temperature.	Beats per Second.
11°	1.64
15°	2.38
17°	2.63
19°	2.98
*21°	4.53
21°	4.55
21°	4.48
25°	5.33
27°	5.4
29°	5.15

$$\frac{\text{Average rate at } 21^\circ}{\text{Rate at } 11^\circ} = 2.76\,; \quad \frac{\text{Rate at } 25^\circ}{\text{Rate at } 15^\circ} = 2.24\,;$$

$$\frac{\text{Rate at } 27^\circ}{\text{Rate at } 17^\circ} = 2.05\,; \quad \frac{\text{Rate at } 29^\circ}{\text{Rate at } 19^\circ} = 2.06.$$

The beat was regular throughout the observations in this experiment. The observations were made in the following order,

21°, 21°, 29°, 27°, 25°, *21°, 19°, 17°, 15°, 11°—hence the rate of beat at 21° was counted three times, twice at the beginning of the experiment and once after taking the animal through a series of temperature-changes none of which were extreme — it will be observed that the three observations at 21° are in very good agreement.

EXPERIMENT 8.

Temperature.	Beats per Second.
11°	1.82
15°	2.95
17°	3.78
19°	4.09
*21°	4.375
21°	4.15 } Average = 4.40
21°	4.65 }
25°	4.67
27°	6.67

$$\frac{\text{Average rate at } 21^\circ}{\text{Rate at } 11^\circ} = 2.41\,; \quad \frac{\text{Rate at } 25^\circ}{\text{Rate at } 15^\circ} = 1.58\,;$$

$$\frac{\text{Rate at } 27^\circ}{\text{Rate at } 17^\circ} = 1.76.$$

The beat was regular throughout the experiment. The organism was taken through the following temperatures in the following order: 21°, 21°, 29° (beats not counted), 27°, 25°, *21°, 19°, 17°, 15°, 11°—hence the rate of beat at 21° was counted three times, twice at the beginning of the experiment and once after taking the animal through a cycle of temperature-changes none of which were extreme—the three determinations of the rate at 21° are in good agreement with each other and with those in experiment 7.

EXPERIMENT 9.

Temperature.	Beats per Second.
19°	3.27
21°	5.12
29°	6.25

The organism was taken through the following temperatures in the following order, 31° (not counted), 29°, 21° and 19°.

$$\frac{\text{Rate at } 29^\circ}{\text{Rate at } 19^\circ} = 1.91.$$

EXPERIMENT 10.

Temperature.	Beats per Second.
29°	6.15
21°	3.06
21°	3.23
19°	2.86

$$\frac{\text{Rate at } 29^\circ}{\text{Rate at } 19^\circ} = 2.15.$$

The beat was regular throughout, but the temperature had been raised above 29° before the observations at 21° were taken.

EXPERIMENT 11.

Temperature.	Beats per Second.
17°	2.38
21°	4.04
27°	5

$$\frac{\text{Rate at } 27^\circ}{\text{Rate at } 17^\circ} = 2.10.$$

The observations were taken in the following order, 21°, 17°, 27°.

EXPERIMENT 12.

Temperature.	Beats per Second.
13°	2.28
21°	4.57
23°	5

$$\frac{\text{Rate at } 23^\circ}{\text{Rate at } 13^\circ} = 2.19.$$

5. The average value of the coefficient $\frac{\text{Rate at } T_{n+10}}{\text{Rate at } T_n}$ for all the observations made was 2.03. The results are therefore such as to confirm Snyder's observations, referred to above, in so far as they apply in general to rhythmically contracting tissues and to lead us to conclude that a chemical reaction is involved — as I have assumed in previous papers.[1]

6. The rate of the beat in different individuals at 21° is remarkably constant, provided they have been treated in the same manner and have not been subjected to any extreme temperatures — this is particularly well shown in experiments 7 and

[1] *Transactions of the Royal Society of South Australia*, Vol. XXIX., p. 47; *Plüger's Arch. f. d. ges. Physiologie*, Bd. 110, s. 610.

8. I have repeatedly confirmed the fact that the rate of the beat at 21° is about 4.5, with a possible variation of about 5 per cent. The organisms were all taken from the same vessel, in which they were kept; but they differed widely in size and development, some containing eggs and others containing well-developed embryos. Ceriodaphnia therefore affords homogeneous material for experiments on the heart-beat.